

STUDIES IN THE ECOLOGY AND BEHAVIOR OF
POLISTES WASPS.

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Among the social Hymenoptera, the ants and bees have attracted the attention of many able investigators. The study of the behavior and ecology of social wasps has, on the other hand, been greatly neglected. We do not need to look very far to explain this attitude; the work is, because of the usual inaccessibility of the nests, difficult to carry on, and also because of the real or fancied danger commonly associated with work of this kind. Two species of social wasps found in this part of the world cover their combs with several sheets of paper, making it impossible for the investigator to see what is going on inside the nest. Another disadvantage for the naturalist is that one species, *Vespa maculata*, builds high in the trees while the other, *Vespa germanica*, makes its nests underground. The *Polistes* wasps are, therefore, because of their open-faced nests, more easily accessible for study,—if the investigator is an adept at climbing over rafters in barns and other such obstacles. But even among *Polistes* wasps only three of the four species found here can be secured without trouble and inconvenience. These are: *Polistes variatus*, *Polistes annularis*, and *Polistes pallipes*. The fourth member of the group, *Polistes rubigenosis*, builds in hollow trees, and rarely crosses the path of the investigator. Any data one may acquire on this last species may be considered a windfall. *Annularis*, though a builder in trees, sometimes builds on low bushes, and sometimes even rears her home under eaves in rural buildings. *Pallipes*, having fully adapted herself to man-made structures, is more often seen; while *variatus*, usually dwelling near or in the earth, is frequently found constructing nests in these same buildings. If some of the notes seem incomplete, one must consider the difficulties under which observations on social wasps are made.

SWARMING OF POLISTES ANNULARIS IN TEMPERATE REGIONS.

In Panama I saw how *Polistes canadensis* var. *panamensis* swarms when the colony becomes too large. I have described elsewhere the breaking up of the colony and the subsequent founding of new colonies by small groups of these swarming wasps.¹ In

¹ Jungle Bees and Wasps of Barro Colorado Island. pp. 97-116, 1933.

the temperate regions a near relative, *Polistes annularis*, is found; so near, in fact, that Dr. Bequaert thinks it is a color variety of *canadensis*. In temperate regions swarming does not occur, but in its stead breaking up of the colony and hibernation takes place.²

For *Polistes annularis*, however, going into hibernation merely delays swarming, for in the spring wasps that have survived the winter come back to the home nest and renew friendships. Then it is that aggregations of few or many individuals swarm to nearby sites to commence nesting operations. The finding of *annularis* colonies in temperate regions wherein actual swarming occurs would do much to strengthen the theory that *annularis* in the north is really *canadensis* of the south. I was fortunate in locating on September 5, 1932, at Moselle, Missouri, a nest which must have had its inception in a manner identical with true swarming in the tropics. This colony, consisting of twelve adult wasps, was under the eaves of a barn; the nest had fifteen newly made shallow cells with very young larvae or with eggs. It was impossible for these adults to have emerged from the shallow cells; they had evidently come in a body from another colony and founded the new nest. These twelve wasps were, no doubt, a portion of a very strong colony under the same eaves only eight feet away. The latter nest was so overloaded with adults that many of them had to resort to piling themselves on top of another to obtain a foothold. With so much overcrowding it was natural for a portion of the population to congregate elsewhere, and, being industrious and of a sociable disposition, it was to be expected that they would stay together and carry on in a new location the nesting activities that were interrupted when they left the old home. One might reasonably suspect that swarming for *Polistes* in temperate regions, as we have seen it, is a vestigial instinct that appears only in times of great overcrowding.

SOUND PRODUCTION AND TROPHALLAXIS.

In a short paper entitled "Trophallaxis in *Polistes pallipes*"³ I record the fact that for the purpose of inducing the flow of saliva in the larva, upon which the adults feed, the latter create certain sounds by rapidly vibrating the body against the open cells. Sound produced by this motion can be heard for several feet from the nest. Whether or not the larvae react to pure sound-waves or only

² Swarming, according to Dr. Wheeler (*The Social Insects*, pp. 224, 1928), does not occur in temperate regions, except in the honey bee and in certain ants (*Formica exsectoides*).

³ *Psyche*, 35: 153-156, 1928.

to the vibration of the cell-walls during this process is not known, but whichever it is it has the power of inducing the larvae to spit up large globules of saliva. There are, however, some variations in the method of body-movement and in the sound that is created. Before recording my observations, I wish to review the method pursued by *pallipes* in the already mentioned paper. There I state that on two occasions an adult was heard to make a prolonged grating noise by rapidly moving the abdomen backwards and forwards against the open cells. On another occasion a wasp with her head at the opening and her antennae curved inside of a cell was rapidly beating it against the wall; her whole body was rhythmically in motion and appeared to actuate the head in the ramming process. These rapid movements of the head against the paper produced a strange sound. In one cell this drumming was repeated six times; and the duration of each round varied from one-fourth to one-half minute. After each trial the queen thrust her head into one of the cells.

In recent years I have again seen, on several occasions, the same behavior in both orphan queens and real queens of *Polistes pallipes*. When so observed the behavior was of three kinds: first, by hammering the head against the edge of a cell; second, by moving the abdomen rapidly from side to side; third, by moving it forwards and backwards, brushing it, in all cases, against the edges of the open cells. I have also observed the same behavior on the part of several adults of *Polistes variatus*. In some cases, as in *pallipes*, the body would swing from side to side; in others it would move forwards and backwards with a jerkily rhythmical motion. In addition, the front legs would occasionally move forwards and backwards in the same rhythmical manner. All of these motions produced the same rasping sound as that recorded for *pallipes*. When one looks into the cells after such a rubbing, beads of saliva can be seen on the mouths of the larvae. The queens always poked their heads into the cells immediately on the cessation of their movements.

That adult wasps have other ways for obtaining the saliva was evidenced in the case of a *pallipes* worker on an orphan nest. When I handed her a half-grown larva of her own species, she chewed it into pulp for some time and it gradually became smaller as she swallowed portions of it. When the last speck (the size of a pin-head) remained, she carried it in open cells and placed it in the mouth of a larva where it immediately disappeared. This behavior seemed very silly at first but I soon discovered that this bit of meat, tiny as it was, set the salivary pumps of the larva in mo-

tion, and soon a big drop of juice made its appearance. The worker reentered the cell, drank it, and was well repaid for the crumb of flesh she gave up to prime the well of saliva.⁴

Male wasps also relish this saliva; I was surprised on another occasion to see a male dive into a cell and emerge with a glistening drop in his mouth, having stolen the saliva from a larva.

COMMUNICATION AMONG POLISTES WASPS.

In observing *Polistes* wasps on the nest, one often notices a clashing of antennae between two individuals, and sometimes a wasp beating the abdomen of another with her antennae may be seen. On p. 233 of this paper, I describe the clashing of antennae between the two founding queens of one nest. Sometimes the movements of the palpi also give one the impression that they function in communication, especially when a returning wasp with a full crop of nectar shares it with others on the nest by mouth to mouth contact. Here the palpi of one wasp often come in contact with those of the other, in a way that indicates communication. Another action that seems to be a signal of some sort is seen when one approaches an *annularis* nest; the members of the population display their nervousness by tilting their abdomens slightly upward, and by standing high on the four hind legs while the two front ones vibrate rapidly with a scissor-like motion. The antennae are held rigidly horizontal during this behavior (Can. Ent., June 1930, pp. 119-120). The distal portions of antennae and parts of the legs are of a conspicuous orange-yellow color, and are in all likelihood a sufficient warning, when in motion, to frighten off any intruder. Since all of the wasps on a nest behave in this way, and since almost all of them act in unison, it seems probable that they are influenced by communication from one to another of some sort.

I have one record that appears to be sign-language; it is that of a worker *variatus* in the act of turning over to the queen a ball of caterpillar meat. The antennae of the worker is thrust out in a stiff manner as she approaches the queen; as the latter is about to receive the meat, she thrusts out her antennae in the same way. When the two pairs meet, they are held together for several seconds before the food changes places. This certainly means something in "wasp language," but just what it is I do not know.

The foregoing notes, while meagre in extent, indicate that communication occurs between adult and adult on the same nest. That

⁴ She was a gluttonous creature, for a few minutes later she was seen to go to one cell and then another, obtaining and eating an egg from each.

there is also communication between adult and larva is indicated in the observations captioned "Sound Production and Tropholaxis."

HIBERNATION AND THE CLUSTER-POINT.

The point at which honeybees begin to cluster is 57° F.⁵ I have often wished to know at what point *Polistes* wasps fall into a state of torpor during their pre-hibernation stage. My notes on the subject are as follows: On a warm day in March, 1930, I brought into the house three hibernating *annularis* queens. They were kept for about ten or twelve days in the living-room; then on March 19, they were taken into an unheated room with the temperature at 43° F. Next day they were found huddled close together in a state of torpor.

I have made several attempts to keep over-wintering wasps until spring (indoors as well as outdoors), but for some reason I have never fully succeeded in doing so. The best results were obtained with five adults brought in from Wickes, Missouri, on August 28, 1930. They were kept in an unheated room but died one on each of the following days: February 1, 8, 20, March 1, 15. In many other attempts, they all died before the end of the same year. One difficulty in making observations of this kind is that one does not know whether he is dealing with young queens or senescent workers, since there is no outward distinction between them. Also, one does not know if feeding when they are active on warm days is good or bad for them. The first part of this problem might be solved by dissection after the wasps die naturally; the second might be solved by keeping the wasps in a refrigerator during hibernation where they are not subjected to warm days and the consequent effects of occasional feeding.

PREPARATION FOR HIBERNATION.

Polistes wasps do not go into hibernation the moment they leave the nest in the autumn; they usually congregate in a more or less social manner at some point near the nest, where they may be seen at night or on cool mornings piled one upon another. I have recorded a few examples of this behavior⁶ for *Polistes pallipes*, *Polistes rubigenosis*, and *Polistes annularis*. I found at that time that the exodus occurs during the day when the temperature is comparatively high, but it usually requires a previous spell of

⁵ Root, A B C and X Y Z of Bee Culture, p. 755, 1920.

⁶ See "An additional note on the behavior of hibernating *Polistes* wasps, Ann. Ent. Soc. Amer., 24: 515-518, 1931.

generally cooler weather to arouse in the wasps an inclination to come together.

The additional notes that follow are not without interest: On one occasion during early August, five large orphan nests of *annularis* were pinned near to one another at the open door of my barn. The orphans that emerged took charge of their respective nests in the usual way and carried on the work. Toward the middle of August, each nest had a large number of adults; during the first week in September, however, I found that many of them had forsaken the nests, and slept night after night one on top of another in a corner of a window-frame ten feet away. Every night I saw from six to nine of them congregating in this corner; gradually the number increased until by September 13, sixteen of them were part of this pyramid-like structure. They finally failed to return and I suspect they found hibernating quarters elsewhere.

At the same time, September 1 to 10, the balance of the population on these five nests, numbering about 150 wasps, had congregated on two of the nests, having completely abandoned the other three. This aggregation has the earmarks of the swarming movements of *Polistes* in the tropics and it also shows that they love the company of one another, "even unto hibernation."

One wonders how the wasps know when to prepare for hibernation; by what uncanny means can they forecast the weather? When the temperature is low, it is too late for flight, and when it is high, they are reluctant to leave the sunshine. Do they sense the oncoming cold, and when the days are yet mild, go forth in search of hibernating places, or do they congregate in some favourable place and then send out scouts to find a location as do the swarms of honeybees?

TEMPORARY SHELTERS OF SITE-HUNTING QUEENS.

Even though the sun shone brightly on April 23, 1936, the day was cold and windy. The official temperature readings for that day at St. Louis, Missouri, were 37° minimum and 60° maximum with a mean temperature of 48° F. But at Glencoe, Missouri, where I studied *Polistes* queens that had sought temporary shelter, I am sure that it was much colder. *Polistes* wasps had evidently been site-hunting during the warm days previous to April 23, for on the nineteenth the maximum temperature was 70°, on the twentieth it was 89° and on the twenty-first, 74°. When the temperature fell to the maximum of 55° and a minimum of 33° on April 22, the site-hunting wasps sought temporary shelter from the cold. I found them in a hibernating condition when I examined a half dozen

abandoned dwellings at Glencoe, Missouri. Ensconced in various niches in these ramshackle buildings were several hundred queens, cold and lethargic. Here about 100 *annularis* queens were found in two groups on old *annularis* nests in the corners of window-frames. On old *pallipes* nests, behind some loose sheets of wall-paper, and in corners of the window-sash, could be found smaller groups of closely huddled *variatus* and *pallipes* queens. Of the 250 to 300 queens observed, only three individuals were found in isolated positions. Among the *annularis* aggregations, I found no other species, but among the aggregations of *pallipes*, I often found a few queens of *variatus*, while among the aggregations of *variatus*, I often found a few queens of *pallipes*.⁷ As expected, there were no males in any of these groups.

A few days earlier, on April 19, toward the close of day, I found at Grubvile, Mo., three such aggregations of *annularis* queens. These had come into a shed for shelter during the night. They probably spent the day in searching for nesting-sites. The nesting season for *polistes* wasps had just about begun, for in this shed I found three tiny nests, each presided over by a queen *variatus*, and each nest having three to six shallow cells.

FRATERNIZING AMONG POLISTES WASPS.

Social wasps are gregarious and *Polistes*, when without companions, often suffer much from loneliness. We only surmise this from their outward behavior. I record here certain observations that support this declaration.

A *pallipes* worker that I had marked as she emerged from an orphan nest, remained on the nest for a week and then disappeared; no others having emerged from the sealed cells up to that time. She was forgotten by me until about ten days later when I noticed her coming to my pond and carrying off gulletful after gulletful of water. Following her over the fence I discovered that she had been adopted by a small *pallipes* colony in my neighbor's shed. She proved to be an efficient worker and, in the new colony, had her craving for company satisfied.

On another occasion I watched a lonely *pallipes* queen for a few days and was surprised on May 17 to see three additional queens on the nest. As I came closer, two of them dropped to the ground. The original queen had been marked in white and one of the three strangers had an orange dot on the thorax. The latter had ruled

⁷ These details are of importance in connection with observations on "The Instinct of Animosity of Queen *Polistes*," and are to be soon published in the *Journal of Comparative Psychology*.

over a nest fifteen inches away which, judging from its neglected condition, she had evidently deserted. I do not know from where the other two came. On another nest in the same barn on which I had left three marked queens the week before, I now found four queens; the new arrival, which was unmarked, dropped to the floor when I approached, while the original three clung tenaciously to the nest. (May 15th is too early in the season for the workers, so I am sure all were queens.)

In another group of farm buildings at Ranken, Mo., I found twenty-one *pallipes* nests, each with one queen, and one with two queens. I returned at night with a flashlight and examined all the nests. I again found one queen on each nest, except the one with two queens; here I now found four queens on the nest, and two nests nearby had none. In a fit of loneliness these two had deserted their own nests, and in a sympathetic way, the reigning queens permitted the lonely widows to remain.

Of course when a queen tolerates the visits of other queens, she is figuratively playing with fire, for it is easy for the visitor to drop her own eggs, cuckoo-bird fashion, into the nest of a sister-queen and thereby start the condition which we know as "social parasitism."

The fact that these visitors "enjoy" the company of others and make advances to obtain it, and also the fact that they are tolerantly received by reigning queens indicates that the gregarious instinct is so strong as to outweigh any antipathy they may sometimes have for one another at certain stages of colony-founding. There is only a short period in the life of a queen *pallipes* when she is alone and away from companions, and it is at a time in early spring when she is founding the nest; in youth she associates with sisters on the nest, her hibernating habits are gregarious, and in early summer she is in the company of her own daughters. Even for such short periods as the early stages of colony-founding, she can hardly bear to be alone, and we find her encouraging visits from other queens, or she herself often going out in quest of company. In certain species, such as *annularis*, the queen is almost never alone, since the nest-founding is often a cooperative venture, and this places her in the company of sister-queens, at the only time in her life when there is a possibility for her to be alone.

BEGINNING OF COLONY-FOUNDING.

I counted about 200 *pallipes* queens flying about the fishermen's shacks at Wickes, Missouri, on April 11, 1930. Although looking for nesting-sites, not one of them had settled down to the business

of building. The only nest seen on that day belonged to a *variatus* queen, and it had six small cells, each with an egg. One half mile away, on the banks of the slough where last year many *annularis* nests were seen in the trees, I found not one new nest, but on several of the old nests, I found from fifteen to thirty-five queens each. They were clustered close together and occasionally additional queens joined those on the nests. At the stream below, several of the queens were filling their gullets with water and flying heavily to the old nests.

Referring to the large number of *pallipes* queens in the shacks, and the large number of *annularis* queens on the nests in the trees, I may state that the winter behavior of both is identical; both spend the winter in hibernation elsewhere, and both, when hibernation has been consummated, return to the old home site, the place of their birth and childhood. In addition to this, both species found their own colonies in the same general region of the old home.

Mid-April seems to be the approximate date (at least for the year 1930) for the commencement of nest-building by *polistes*, for on April 12 and 13 I noticed two *pallipes* queens and one *annularis* queen reconnoitering for nesting-sites about my premises at Kirkwood, and a few days later I discovered that all three had commenced to build there.

BEHAVIOR OF QUEENS WHEN TWO OR MORE ARE FOUNDRESSES OF A NEST

It is a difficult task to learn the relative importance of each queen when two or more are foundresses of one nest. Do all queens share equally in the work and in egg-laying or do some of them sink into the role of workers? Should we wish to further complicate the unraveling of this skein, we might ask if it is not likely that the overworked queen becomes sterile (ovarian castration), and is thereby reduced, physiologically, to a worker? These problems bear heavily on the unraveling of the tangled mesh of psychological and physiological evolution. Difficult as the problem is, it is worthy of much effort and study.

I have only a few notes on this subject: One *pallipes* nest that I observed at the beginning of the season, April 28, had three females in charge, and from that date to June 3, they continued to get along peaceably. At the earlier date the nest had 16 cells, and on May 27, it had 32 cells. A week later, on June 3, it still contained the same number of cells. These three queens were marked and observed from time to time; their reciprocal relations seemed to be practically the same as between one queen and two workers; one

was constantly in charge, but the others would come and go at will. The observations seemed to indicate that the two females were vassals of the one that stayed on the nest and assumed the queenly duties. The queens would very often communicate with one another. One would deliberately walk up to another and administer a certain number of blows with her antennae on that of the listener. And too, one queen would often pose before the other and rapidly vibrate the forelegs in a scissor-like motion. This behavior certainly indicates communication; the acts were done with apparent deliberation and purpose. Long after the arrival of workers on the nests, these three marked wasps continued their harmonious cohabitation.

THE TIME SPENT ON THE NEST DURING ITS EARLY STAGES
BY PALLIPES QUEENS

The day was warm and sunny on May 20, 1932, and I observed, along with some other work I was doing nearby, the comings and goings of queens on twelve nests. Some of them left the nest but once during the day; others as many as four or five times; none of them left the nest more than five times. All came in apparently empty handed; at least no building-pulp or caterpillar-meat was seen in their jaws. They may have brought in nectar, however, and placed it in the cells, for often a returning queen would poke her head into a cell and keep it there for several minutes.

THE SIZE OF ANNULARIS NESTS IN RELATION TO THE NUMBER OF
QUEENS THAT FOUND THE COLONY

One notices much variation in the size of *annularis* nests. Sometimes at the end of the season, they are quite small; sometimes quite large. The size of the nest is in proportion to the number of queens that found it. Colonies with only one queen have small nests; those with many queens have large nests. The largest nest I have seen of this species was one exhibited in a store at Allenton, Missouri; I knew it to be of this species by the position of the pedicle. It measured 11 x 11 inches and contained 1936 cells. The normal size of the nest is probably very much like that of four nests which I took on low bushes at Ranken, Missouri. It was almost at the end of the season (August 10), and the nests contained 268, 277, 287, and 292 cells respectively. But no one knows how many queens had a hand in the founding of these nests.⁸

That there is a very definite correlation between the size of the

⁸ Pierce (Bull. U. S. Nat. Mus., No. 66, 17, 1909) took two *annularis* nests in Texas; one had 1575 cells and the other had 1212 cells.

nest and the number of founding queens is proven by the following data gathered early in the year before the workers were born.

Date	Location	No. Nests Observed	Numbers of Nests with—			
			1 Queen	2 Queens	3 Queens	4 Queens
5/5/30	Sullivan, Mo.	3	12 cells	23 cells		90 cells
5/9/30	Cliff Cave, Mo.	3		32 cells	40 cells	45 cells
4/20/32	Weingarten, Mo.	8	4, 6, 6, 9, 9 cells	19, 20 cells		38 cells

Thus we see, at least early in the year, that two queens on a nest will, on an average, more than double the cell production over those with one queen, and four queens on a nest will often quadruple it.

The work of cell building for this and other species of *Polistes* does not go on indefinitely; the period comes, at one time or another, when building operations stop and attention is directed to the feeding and nursing of the young. I was able to note the amount of cell building done between June 13 and July 6 by one colony that had three queens. On June 13, the nest had 35 cells with larvae or eggs, and 9 sealed cells with pupae, making a total of forty-four cells. On July 6, after a period of about twenty-three days, when I counted them, I found eighty-five cells with eggs or larvae and seventeen cells with pupae, making a total of 102 cells; thus showing that queens and workers were responsible for making fifty-eight cells during that period. I might say in passing (even though this fact has nothing to do with nest building) that in the twelve big empty cells in the center of the nest (from which workers had recently emerged), I found each one supplied with an egg, thus confirming previous records that certain cells (especially the original ones) are used more than once for young.

THE SIZE OF PALLIPES NESTS IN RELATION TO THE NUMBER OF QUEENS THAT FOUND THE COLONY.

Often several queens cooperate in the founding of *annularis* colonies, but it is only on rare occasions that one finds a nest of *pallipes* founded by more than one queen. Finding a nest with two queens gave me an opportunity to compare the growth of a nest with two queens with that of nests having only one queen. The table below gives the data on the amount of work done by each of twenty-two queens on twenty-two nests, and also the work done by two queens on one nest.

Date.	Location.	No. Nests Observed.	Number of Cells.									
			6	8	10	12	14	16	18	20	50	
5/5	Sullivan, Mo.	1 queen each on 6 nests.										
5/18	Ranken, Mo.	1 queen each on 16 nests.	1		1	1	1	1	1			
5/18	Ranken, Mo.	2 queens on 1 nest		2	2	3	4	2	2	1		
											1	

Here we see that nests with one queen had, on these dates, from six to twenty cells; and that one nest with two queens had fifty cells, the latter pair working alone, and doing, therefore, about three times as much work as the average queen. This indicates that both wasps did the manual labor and that this project is truly a cooperative venture; for if one wasp was vassal and the other a non-working queen, I doubt if so much work would have been accomplished.

(To be continued)

Notes on Preparation Technique.—I find that by cross-ruling a sheet of fine stiff paper with a broad lettering pen (such as a C-4 Speedball) and then cutting along the middle of the lines produces neat determination labels in short order. I make my labels 10 x 20 cm.

It does not seem to be generally known that immersion in xylol will nicely degrease specimens. A lightly greased specimen will be put in fine shape in a few minutes without matting hairs. The liquid may be used repeatedly for some time, and has no effect on pointed specimens glued with acetic gelatin. Nor is it generally known that concentrated ammonia water applied with a pointed brush will quickly relax specimens in order to move a part obscuring necessary characters, etc. I use the ammonia applied to the whole insect to relax the hypopygium of Diptera. I wet the fly and put it in a relaxing chamber for about a half hour, which is usually sufficient.—GEORGE STEYSKAL, Detroit, Mich.